Predator-Prey Reactions Between Two Marine Prosobranch Gastropods

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INTRODUCTION

Specific behavior patterns elicited from many mollusks by the touch of certain starfish or extracts from them have been demonstrated in experiments performed under laboratory conditions (Bullock, 1953; Margolin, 1964a). These experiments indicate that such actions could function in nature as effective escape reactions to potential predators. Such escape reactions may be demonstrated with many prosobranch gastropods, particularly intertidal forms such as limpets and turban snails. Escape reactions are not restricted to gastropods among the mollusca but are also shown by pectens and cockles (Ray, 1959) to the presence of certain starfish.

While the experimental evidenee of the effectiveness of these reactions is convincing, there is a lack of information on the spontaneous occurrence of these reactions in predator-prey confrontations under entirely natural conditions. Margolin, 1964b, found that the escape response shown by *Acmaea* to starfish did not prevent their eventual capture in an aquarium and concluded that his results may indicate a lack of survival value for the flight reaction, at least in the laboratory. Feder, 1959, on the other hand, found that gastropods were not eaten in the field by *Pisaster ochraceus* in proportion to their numbers and concluded that the known escape responses of *Acmaea* spp., *Tegula* spp., and *Haliotis* spp. may be protective to the species. Field observations on spontaneous prey-predator contacts would make possible an evaluation of the effectiveness of these mechanisms in nature and their importance as selective factors in the evolution of the mollusks involved.

Most predatory marine gastropods feed upon sedentary prey organisms such as bivalves, barnacles, coelenterates, tunicates, and worms. Consequently, the more complicated aspects of their feeding behavior usually involve the mechanisms used in detecting food, holding and opening the shells of prey or boring into them, rather than the pursuit and capture of prey. Notable exceptions are the stalking and capture of fishes by *Conus* spp. observed by Kohn, 1961, and the trailing of prey species by *Navanax inermis* observed by Paine, 1963. Naticids are common predatory marine gastropods of soft bottoms which feed principally upon clams, but also upon other gastropods. Information on their method of feeding upon clams has been summarized by Fretter & Graham, 1962. Clams are held in the extensive foot of the naticid while a hole is bored in the shell. Capture and feeding take place below the surface of the bottom.

An example of active pursuit by a naticid of a gastropod prey species, together with an escape reaction by the prey was observed under field conditions on the Pacific coast of Costa Rica. Predator induced escape reactions involving two gastropod species appear to have been observed in the field and described briefly only once before (Clark, 1958), and the observations recorded here provide some information on how naticids capture other, active gastropods in nature.

The field observations were made on an intertidal flat of sandy mud near the town of Golfito, Costa Rica, on the Golfo Dulce (83° 10′ W, 8° 38′ N). According to Keen, 1960, both species involved are common on intertidal mud flats from the Gulf of California to Ecuador, which should permit detailed anlysis of their behavior later. The predator species involved is a variant of *Natica (Natica) chemnitzii* Pfeiffer, 1840, called *Natica unifasciata,* which is characterized by one white band on the upper part of the whorls of the brownish shell. There are unresolved taxonomic difficulties with this species complex. Some of the specimens used have been deposited in the collections of the California Academy of Sciences so that the taxonomic status of the *Natica* species involved may be verified at a later time. The prey snail is readily identified as *Nassarius (Arcularia) luteostoma* (Broderip & Sowerby, 1829).

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PREY CAPTURED BY *Natica unifasciata*

Natica unifasciata is abundant on the mud flats at Golfito, crawling rapidly about on the surface at low tide. The gross morphology of this naticid is typical of the family. There is an extensive, wide anteriorly extended portion of the foot (the propodium) and a large, flat ventral mesopodium which is expanded posteriorly into a thin, widened posteriorly trailing portion. Many *N. unifasciata* were found crawling about with a clam, covered with thick sticky material, firmly stuck to the underside of the posterior foot lobe which covered it like a sucker. The largest snails found had shell diameters of about 2 cm and a total length of the body when extended of about 5 cm. Most of the clams being carried about were small in relation to the snail and scarcely protruded from beneath the posterior foot lobe. However, some were dragging clams of about 4 cm shell length, much larger than the posterior foot lobe; thus demonstrating the effectiveness of the hold exerted on the prey by the bottom surface of the foot.

Natica unifasciata were also found carrying *Nassarius luteostoma.* The nassarid is small enough to be completely covered by the foot. It is held in an inpocketing of the bottom surface and is thus virtually entirely enveloped. This produces a lump in the dorsal surface of the posterior foot lobe, permitting those *Natica* carrying nassarids to be identified and followed. *Natica* carrying either a clam or *Nassarius* could be followed as they crawled about the surface for a distance of one or two feet, after which they pushed into the mud and slowly burrowed from sight, carrying the captured prey. If they are disturbed while on the surface, they will continue to crawl about, but buried *Natica* immediately re-burrowed when uncovered. Capture and carrying of the prey across the surface appears to be a peculiarity of this naticid, but it burrows with its prey, and like other members of the family, feeds upon it below the surface.

The method of capture of the prey snail and the manner in which prey are attached to the foot were also observed in the field as they occurred spontaneously. *Natica unifasciata* crawls rapidly about the mud flat, apparently without direction. If the prey snail was contacted directly by the anterior foot lobe, capture was immediate. When the trail left in the mud by a crawling *Nassarius* was crossed, the *Natica* immediately began to follow it and overtook the slower crawling nassarid if the proper direction was chosen. This was observed several times as *Natica* crossed the trails of nassarids about 6 inches away. The details of escape reactions of the prey upon contact are described below. When contact is made, the nassarid becomes very active and moves rapidly and erratically. *Natica unifasciata* is able to sense the changes in direction of the nassarid trail and accurately pursues them. Usually several attempts at capture were tried before a successful hold was obtained upon the prey. Capture is effected by lifting the wide propodium above the surface of the mud with the thin, flat edges extended laterally, and bringing it down rapidly over the small prey snail. If the prey is successfully covered, the front edge of the propodium is curved down and rolled partially around the struggling nassarid. As the prey is slowly enrolled in the propodium, the *Natica* falls on its side as the more posterior portions of the foot are brought ventral and forward, free of the substrate. The head area is brought ventral and posterior, meeting the posterior portion of the foot curving forward. The prey is thus entirely surrounded by the foot. The long axis of the shell of the nassarid is held across the width of the anterior part of the foot and is slowly rotated as it is moved posteriorly. As it is rolled by the propodium, it is covered with a thick, sticky mucus. Nassarids examined at this point had stopped struggling and were withdrawn into their shells. The prey is slowly transferred poteriorly to the apron-like posterior foot lobe which holds it in a sucker-like fashion. As the prey reaches the posterior end of the foot, the *Natica* rights itself with the propodium and begins to crawl away, carrying the prey. Clams being carried were also found completely covered with this thick mucus, which is apparently important in both subduing the more active prey and maintaining the hold by the posterior foot. Capture of a second prey individual was not observed to occur naturally. All *Natica* carrying prey that were followed eventually burrowed below the surface.

In the field *Natica* pursued *Nassarius* placed in their immediate vicinity. Other snails found on the mud flat and placed in contact with the *Natica* were not taken. Clams removed from the foot lobe and left next to the *Natica* were re-secured by the propodium and re-attached to the posterior foot lobe.

Specimens of *Natica, Nassarius,* and several other species of prosobranchs from the mud flat were placed together in bowls of sea water. The *Natica* continued to follow *Nassarius* about, but showed no reactions to the other species of snails when they touched them, even when left together with them overnight. A variety of sizes including individuals of the size of the *Nassarius* were used in this experiment. *Natica unifasciata* does not react to shells of *Nassarius luteostoma* occupied by small hermit crabs.

ESCAPE REACTIONS OF *Nassarius luteostoma*

The behavior of *Nassarius luteostoma* when confronted with *Natica unifasciata* was observed as spontaneous contacts were made by undisturbed animals in the field and also by placing the species together both on the mud flat and in bowls of sea water. The reactions are the same in all cases.

It is evident from the precise directionality of its pursuit that the *Natica* can sense some substance left by the nassarid in its trail across the mud. The nassarid also appears to be able to detect the predator by chemosensory means. *Nassarius* placed in small puddles on the beach containing several *Natica* very rapidly crawled out and away. When the two species are placed together in bowls, the nassarids slowly crawl about at random and occasionally toward a *Natica*. However, if they approach a *Natica* within about $1\frac{1}{2}$ to 2 cm, they will turn and crawl rapidly away.

If *Natica* is picked up, it will slowly withdraw into the shell, releasing a little water from the pallial cavity and the foot surface as it does so. This fluid was collected with a pipette and released near quiet nassarids in a bowl of sea water. The fluid invariably elicited the entire series of escape reactions described in detail below, without any actual contact with the body of a *Natica*. A flow of ordinary sea water is without effect.

These observations establish that the *Nassarius* can sense the predator a short distance away by some chemosensory means and will then begin to crawl away rapidly. Closer contact with a *Natica* produces more active behavior similar to the escape reactions shown by other prosobranchs to starfishes.

If any of the parts of the body of *Nassarius luteostoma* come into contact with those of *Natica*, the *Nassarius* immediately begins a series of rapid actions. In nature, the course of these actions proceeds as follows. Upon contact, the nassarid extends the foot and head from the shell maximally and usually falls upon its side as the shell is swung from side to side. The foot assumes an elongate, slender shape and the head and foot region thrashes about rapidly. The elongated foot acts as a lever and its violent jerks from side to side move the snail erratically, but rapidly, over a distance of about three inches. If this violent leaping removes the nassarid from the vicinity of the *Natica*, it then rights itself and crawls rapidly away, with the shell held high over the foot. After crawling about six inches, it slows and lowering the shell, resumes its slower undisturbed crawling. One contact with *Natica* will induce very active escape behavior of about 30 seconds duration.

Efforts made to demonstrate fatigue of the escape reaction were not successful. Nassarids were touched against *Natica* held in bowls with them. The entire sequence of actions was induced repeatedly, without failure, even if repeated at intervals of one minute, as soon as the nassarid stopped the thrashing action induced by earlier contacts. Gradual fatigue of the response of limpets to starfishes by repeated frequent contact was demonstrated by Margolin, 1964a. Individuals of *Nassarius luteostoma* continued to react violently as long as they were held against the *Natica*.

DISCUSSION AND CONCLUSIONS

Natica unifasciata carries both clam and snail prey for some distance about on the surface before feeding and in this behavior differs from related species which capture and feed on clams below the surface. Other naticids also cover clam prey with mucus and are able to drag the prey with the foot down below the surface, but apparently not for any distance across the surface (Fretter & Graham, 1962). There is no comparable information available on the method used by other Naticidae to capture gastropod prey. The carrying of the snail prey by *Natica unifasciata* is related to its pursuit and capture of active *Nassarius luteostoma* on the surface of the mud flat, and its extension to carrying clams, which might be taken under the surface, is probably secondary. The observations indicate that the mechanism used by *Natica* to sense its prey is sufficiently sensitive to permit the detection and pursuit of prey capable of active avoidance. It is probable that the capture of gastropods by other members of the Naticidae is different from the slow means which they use on clams.

The observations made under natural field conditions demonstrate that *Nassarius luteostoma* possesses an escape reaction mechanism toward its predator, *Natica unifasciata,* which can allow the *Nassarius* to successfully escape attack by its predator. However, the initial violent movements of the reaction do not always move the *Nassarius* away from the *Natica,* and thus may fail to prevent capture. Such failure was observed directly in the field and is also demonstrated by the number of *Natica* found carrying captured *Nassarius.* It may be concluded that escape reactions in gastropods produce some success under natural conditions and are thus of selective importance. They do not, however, insure individual survival.

Escape reactions, mediated by chemoreception, are known for other species of *Nassarius,* which, however, respond to the presence of or extracts from starfishes predatory on the *Nassarius* rather than to another snail.

The literature on the reaction of these *Nassarius* species has recently been summarized by both KOHN (1961) and FRETTER & GRAHAM (1962). The use of the foot in the movements involved in the reaction is essentially the same as in *N. luteostoma,* even though induced by very different predators. The presence in *N. luteostoma* of a specific escape reaction to a predatory gastropod indicates that these reactions in prosobranchs are developed in response to predators which are relatively slow moving and not exclusively to carnivorous starfish. The sensory basis in both cases is chemosensory detection of material released by the predator.

Flight reactions of normally sedentary animals would not be expected to be an efficient response to fast moving predators such as fishes and indeed, only slow moving predators are involved in the known flight reactions of marine invertebrates. This is the most important common characteristic of the reactions between otherwise diverse predator-prey pairs such as *Acolidia/Stomphia* (ROBSON, 1963), *Natica/Nassarius* and *Pisaster brevispinus/Dendraster excentricus* (MACGINITIE & MACGINITIE, 1949). REESE (1964), in a general review of the behavior of marine animals, also concluded on different grounds that convergence of adaptive behavior patterns in species confronted with similar problems is a general phenomenon.

Reactions of herbivorous gastropods to predatory snails were described for a number of species by CLARK (1958). One of these reactions was observed as it occurred spontaneously in the field and bears some resemblance to the *Natica/Nassarius* reaction. CLARK observed that when the thaisid whelk *Lepsia haustrum* touched the trochid *Melagraphia aethiops* the latter exhibited rapid reactions which involved violent swinging of the body in a manner similar to that described here for *Nassarius.* However, contact between the two snails was apparently random and the predatory *Lepsia* was not observed to pursue the trochid or feed upon it.

It was not clear whether the responses shown by the other species studied by CLARK in the laboratory were specific responses to a snail predatory on these species, and operative under natural conditions or whether the responses to the carnivorous snails were fortuitous and not of survival importance in nature. The species studied by CLARK also showed escape responses to carnivorous starfishes, and he found no correlation between the co-occurrence of the snail species and reactions between them. Some pairs of snail species reacted which probably never meet in nature. In other cases (MARGOLIN, 1964a) escape reactions have been demonstrated experimentally between snails and starfishes which either never take the reacting species naturally or which do not occur in the same habitat. ROBSON (1963) showed that an escape reaction of the anemone *Stomphia coccinea* to its predator, *Aeolidia papillosa* is also evoked by certain starfishes which are not predators of the anemone, but which also produce a substance which will induce the reaction. In these cases, the reactions seem to have been developed as a specific adaptive response in one prey-predator relationship, and are operative in response to species which are not normal predators because of chance production by these species of substances which will elicit the response. No such ambiguity is present in the relation between *Natica* and *Nassarius* described here. Observation in the natural habitat demonstrated that a prey-predator relation exists between the two species and that the reaction can allow successful escape from the attacking predator and is thus adaptive. The ecological significance of the many flight reactions of marine invertebrates demonstrated under laboratory conditions cannot be evaluated until these observations are extended to observations of the species involved under entirely natural field conditions.

An instance of an apparent escape reaction shown by one snail to another carnivorous snail species was mentioned by PETERS (1964). In this case *Littorina planaxis* showed an escape flight from the carnivorous *Acanthina spirata* in the laboratory and also to a substance released into the water by the predator, as does *Nassarius* to the fluid from *Natica. Acanthina* and *Littorina* are known to occur in the same general habitat on the Pacific coast of North America, but a prey-predator relationship under natural conditions has not been demonstrated.

Similarly, ROBERTSON (1961) found that in an aquarium, *Strombus gigas, S. costatus* and *S. raninus* leaped violently away from the carnivorous snail, *Fasciolaria tulipa.* The escape reaction was not observed under natural conditions. However, in this case a prey-predator relation was established by field observation. ROBERTSON frequently found *F. tulipa* feeding on *S. gigas* and considered it to be the principal predator of *Strombus* at Bimini. It would appear that in this case the escape reaction is only partially effective against attack by the predator, as it is in the *Natica-Nassarius* case.

SUMMARY

Natica chemnitzii, a predator of both clams and *Nassarius luteostoma* on the mud flats at Golfito, Costa Rica, carries its captured prey across the surface of the flat by holding them with the posterior lobe of the foot.

Natica can detect and follow the trails of *Nassarius* across the mud. It captures the snail by throwing the wide anterior end of the foot over the prey, rolling it in a sticky mucus and then holding it securely by the sucker-like action of the posterior foot lobe.

Nassarius luteostoma can detect the presence of *Natica* through the water at a short distance and exhibits specific escape reactions to the presence or touch of *Natica*. Under natural conditions these quick actions often but not invariably allow the *Nassarius* to escape the pursuing predator.

Note added in proof:

Yarnall (1964) has recently investigated the response of *Tegula funebralis* to *Acanthina spirata* and *Thais emarginata*, both carnivorous prosobranchs from the same general habitat as the *Tegula*. The behavioral response of *T. funebralis* to pieces of the foot of these carnivores was considered essentially the same as the known escape reaction of *Tegula* spp. to starfish normally predatory on *Tegula*. The exact nature and function of this response, its spontaneous occurrence in the habitat and the existence of a true predator-prey relationship were not sufficiently established to make possible a comparison with the *Natica-Nassarius* interaction and others mentioned here.

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